PAN-PACIFIC ENTOMOLOGIST
65(3), 1989, pp. 302–309

A Scanning Electron Microscopy Study of the Mouthparts of *Paraponera clavata* (Hymenoptera: Formicidae)

John H. Whiting, Jr., Hal L. Black, and Clive D. Jorgensen

Department of Zoology, 167 WIDB, Brigham Young University, Provo, Utah 84602.

Abstract.—Nine specimens of *Paraponera clavata* were collected on Barro Colorado Island, Panama, and their mouthparts studied using scanning electron microscopy. Structures of the mouth that enable *P. clavata* to form and carry visible droplets of nectar were characterized; including the mandibles, labrum, stipetes, and glossae. The glossae were photographed and analyzed. The scanning electron micrographs in this study of the intact mouthparts of *P. clavata* are important additions to earlier morphological studies of the mouthparts of *P. clavata* that utilized light microscopy and line drawings.

Paraponera clavata (Fabricius) is a large tropical ponerine ant which harvests nectar from the forest canopy and returns it to the nest suspended as a droplet between its mandibles (Bennett and Breed, 1985; Hermann, 1975; Janzen and Carroll, 1983; McCluskey and Brown, 1972; Young and Hermann, 1980). Only two other species of ponerines, *Ectatomma ruidum* and *E. odontomachus,* are known to collect a liquid food source (Breed and Bennett, 1985). *P. clavata* therefore, departs from the typical ponerine condition of entomophagous feeding.

Anatomical and comparative descriptions of mouthparts of insects have been reported by Crampton (1923, 1928), Huxley (1878), Janet (1899, 1904, 1905), Liu (1925) and more recently by Duporte (1967), Snodgrass (1956), and Steinmann and Zombori (1981). Comparative descriptions of the mouthparts of ants have been made by Bugnion (1924, 1925, 1930), Eisner and Happ (1962), Marcus (1944), and Matsuda (1965). Such anatomical and morphological studies, which required a light microscope, drawing tubes, patience, and artistic skill, provided drawings which serve as important references for systematic classification. However, such drawings required a substantial time investment and the results relied heavily on the skill and the scientific insight of the worker.

Gotwald (1969) described the mouthparts of *P. clavata* in his comparative study of the mouthparts of 104 species of ants. His drawings depicted the dissected mouthparts as they appear when flattened under a glass coverslip. Although Gotwald's study was excellent, it was not intended to give a comprehensive characterization of *P. clavata* mouthparts and was somewhat limited by the line drawing technique he used. Hermann et al. (1984) conducted a comparative study of the anatomy and chemistry of the mandibular gland in *P. clavata* and *Dinoponera grandis.* They limited their diagrams of *P. clavata* and *D. grandis* strictly to the mandibular venom glands and sting apparatuses.

Cromroy et al. (1987), Harrison (1987), and Szlzytko and Bottorf (1987) have used scanning electron microscopy (SEM) extensively to characterize several new species of insects and arthropods. Michener and Brooks (1984) used SEM in a taxonomic study that examined the proboscides of 290 species of bees, and Peng and Marston (1986) studied the honey bee proventriculus with SEM. Nelson and Baumann (1987) used SEM to characterize the male terminalia of stoneflies. Erickson et al. (1986) bypassed traditional methods of studying insect anatomy and did a complete anatomical study of the honey bee using SEM.

In this study we characterize the intact mouthparts of *P. clavata* with high resolution and magnification using scanning electron microscopy, and discuss those features that aid in droplet formation and suspension.

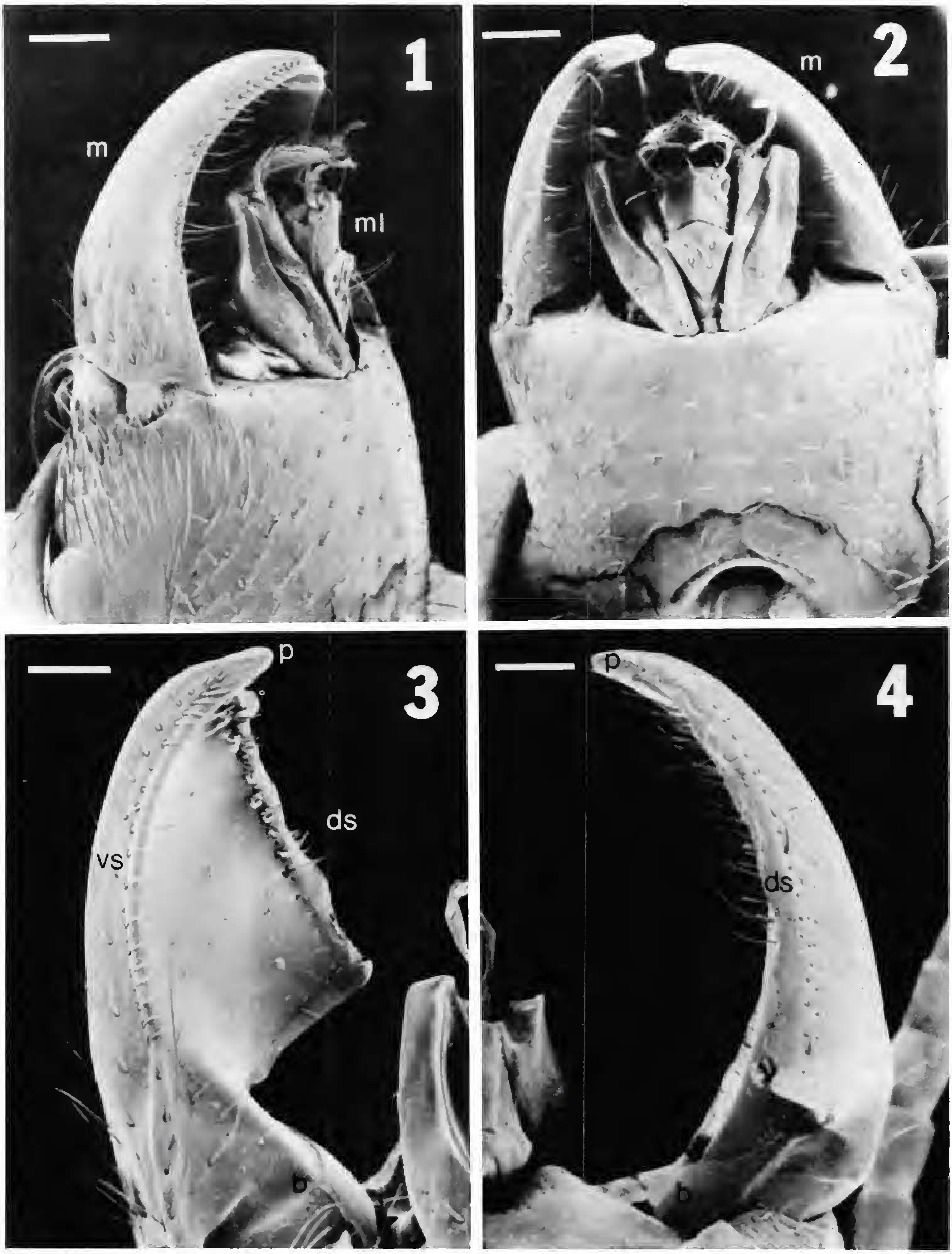
Methods

Specimens of *P. clavata* used for this study were collected on Barro Colorado Island, Panama, and preserved in 70% ETOH. Techniques used in preparing the ants for scanning electron microscopy closely followed those of Nelson and Baumann (1987). Heads of the ants were dissected in 95% ETOH and the mandibles pried open. The heads were dehydrated in a series of three 10-min absolute ethanol washings, followed by three 10-min washings in anhydrous acetone. Dehydrated specimens were critical point dried in a Sorvall critical point drying apparatus using CO_2, mounted on aluminum studs with double-sided tape, and coated with gold using a Polaron gold-coating apparatus. Charge of the specimen was reduced, and conduction between the specimen and the stud was increased, by adding a droplet of liquid silver to the base of the head at the point of specimen–stud attachment. Scanning electron micrographs were taken with an AMRay 1000 scanning electron microscope.

Results and Discussion

SEM is rapidly replacing the line drawing technique as the preferred method for conducting morphological and anatomical studies of new species, or adding to the characterizations of previously described species. A comparison of Erickson and his colleagues' (1986) SEM study of the anatomy of the honey bee, and a similar line drawing study conducted by Snodgrass (1956), revealed some benefits of SEM. Erickson's micrographs of the honey bee were clear and concise. The high magnification, high resolution, and depth of field of SEM enabled Erickson to characterize honey bee morphology more precisely.

Similarly, SEM used in this study provided high resolution, and high magnification micrographs of intact *P. clavata* mouthparts, that enhanced the morphological detail provided earlier by Gotwald (1969). Figures 1 and 2 show the intact mouthparts as they appear in relation to each other. The mandibles gently curve over the intact maxillo-labial apparatus, forming an umbrella-like shield. The articulation of the mandibles is dorso-ventral and the mandibles are able to move in one plane only, toward and away from the median longitudinal axis of the body (Matsuda, 1965). When closed, the mandibles overlap each other with the right mandible most often overlapping the left. Medially directed setae line the ventral side of the mandible (Fig. 3). The mandible is relatively broad and long in comparison to other ants (Gotwald, 1969), with a curving-cupping shape. Short spine-like setae also line the immediate inner edge of the distal side of the mandible



Figures 1–4. Mouthparts of *Paraponera clavata* with mandibles (m), ventral side (vs), distal side (ds), point (p), and base (b) labeled. 1. Right mandible and maxillo-labial apparatus, lateral view (bar = 1.6×10^{-3} m). 2. Mandibles and maxillo-labial apparatus, ventral view (bar = 1.6×10^{-3} m). 3. Right mandible, ventral view (bar = 4.5×10^{-4} m). 4. Right mandible, dorsal view (bar = 4.7×10^{-4} m).

(Figs. 3, 4). The distal side and ventral side of the mandible converge forming a sharp point (Figs. 3, 4). The base of the mandible is heavy and rounded. The circular curvature of the mandible is pronounced (Figs. 3, 4). Prominent features of the maxillo-labial apparatus are the stipes, maxillary palpi, labial palpi, galea, and the premental shield (Figs. 5, 6). The maxillo-labial apparatus is supported ventrally by the hypostomal bridge. The glossa can be retracted inward toward the hypostoma, leaving a folded indentation between the maxillary and labial palpi. Four characteristic prominent setae extend ventrally from the premental shield.

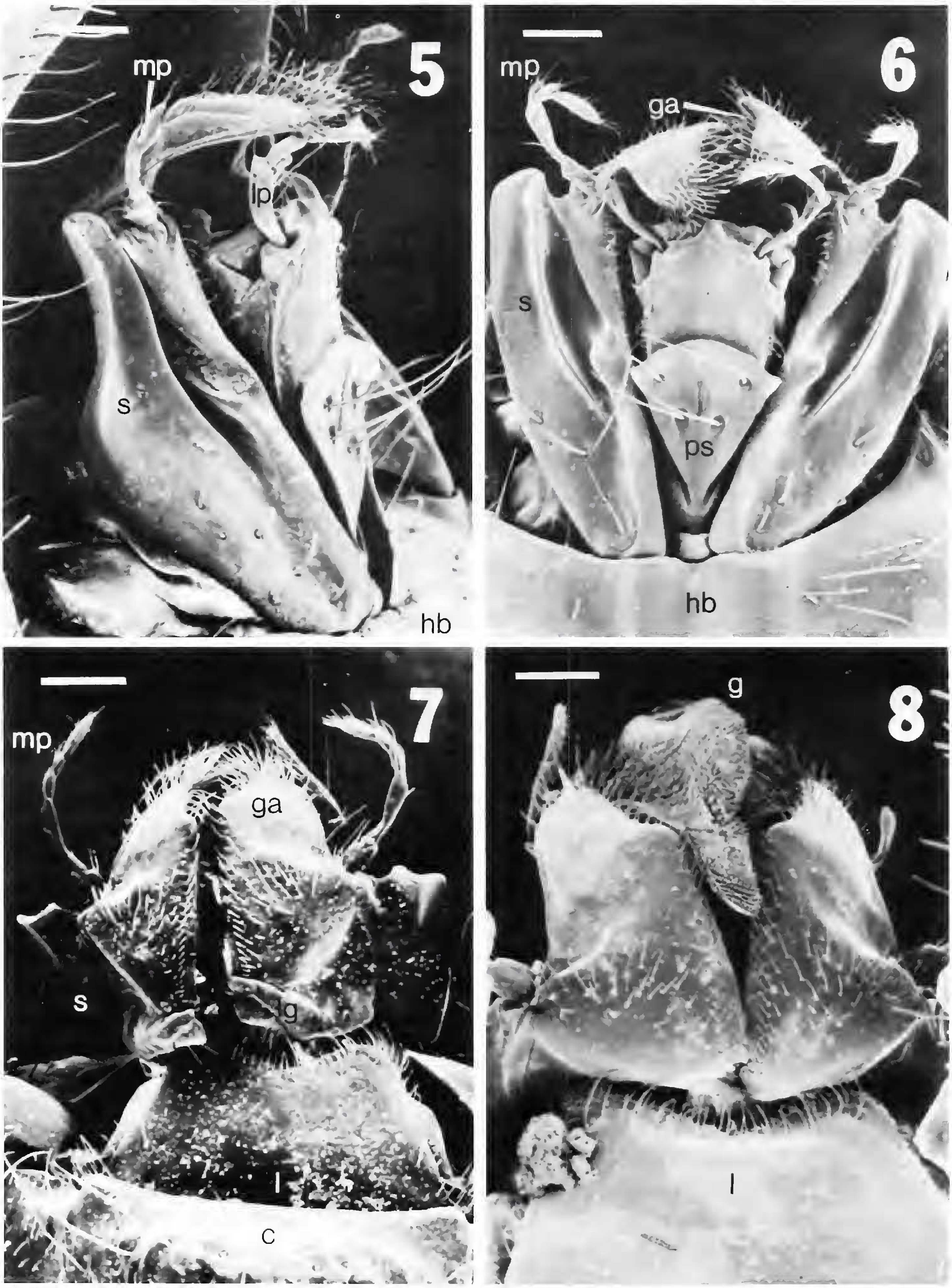
A dorsal view of the maxillo-labial apparatus is shown with the glossa retracted (Fig. 7) and extended (Fig. 8). Prominent features of the maxillo-labial apparatus are the labrum, galea, lacinial gonia, and stipes. The maxillo-labial apparatus is supported dorsally by the clypeus. The labrum is medially cleft forming two distal margins, and is lined on the distal edge with setae. The proximal edge of the lacinial gonia is also lined with setae, forming the lacinial comb.

A ventral view of the maxillo-labial apparatus is shown in Figure 9, with the glossa extended, and the mandibles partially open. The glossa protrudes forward and downward and is flanked by the galea (Fig. 10). At lower magnifications, the glossa is ridge-like and raspy. Stout, rounded setae form symmetrically parallel horizontal lines. The distal edge of the glossa is lined with a ridge of modified setae, narrow at the base and sharp at the tip.

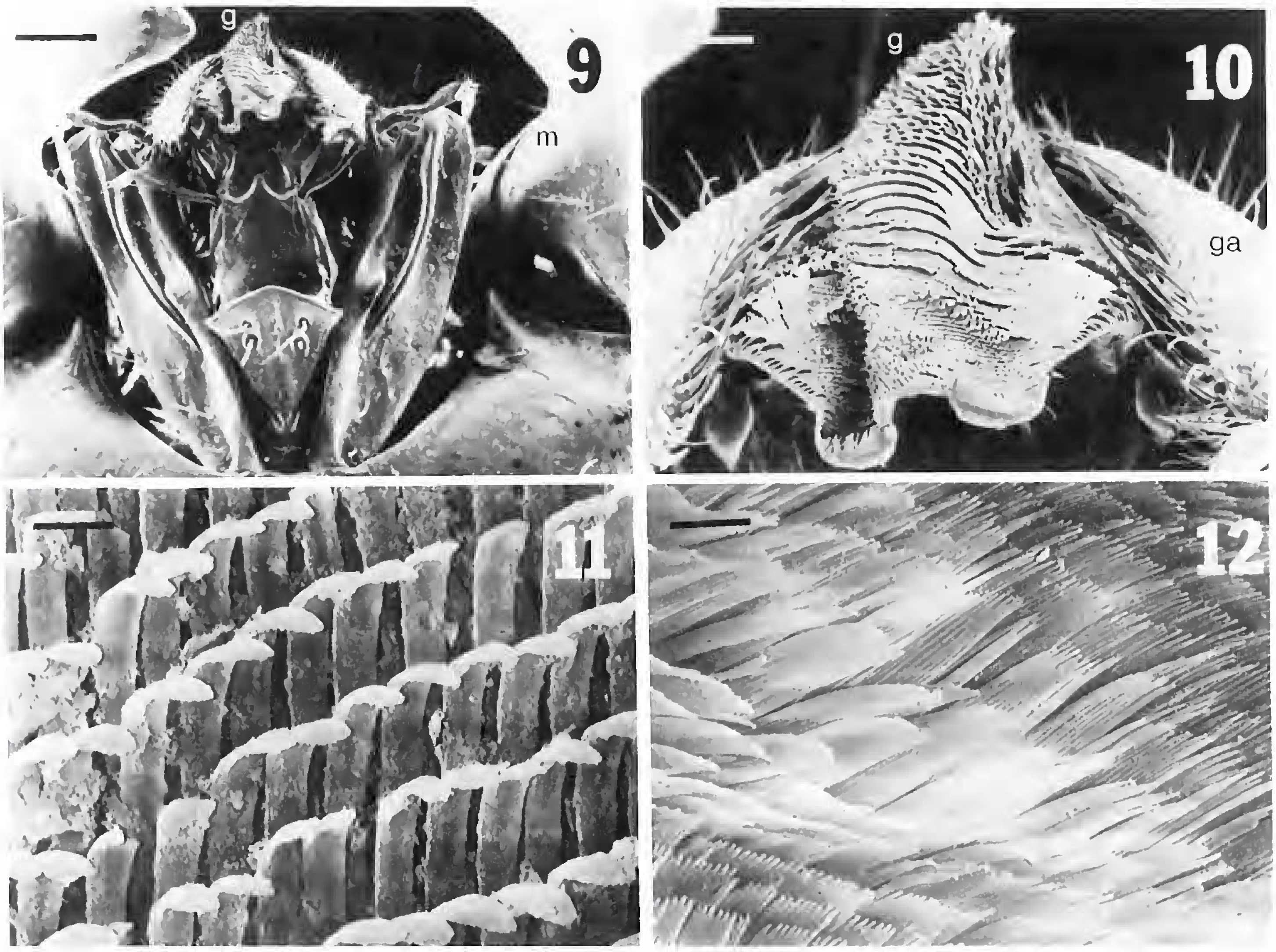
The intricate detail of the glossal setae is apparent at higher magnification (Fig. 11). The setae are flat, widening at the end with curved, cup-like tips. The cup-like tips curve upward toward the hypostoma. The glossa is flanked by the subglossal brush (Fig. 12) which consists of thin, pointed, feather-like setae, in overlapping layers. The pointed, feathery setae of the subglossal brush sharply contrast with the rounded cup-like glossal setae.

Mouthparts which probably permit *P. clavata* to transport bubbles of nectar or other liquids are the mandibles, labrum, stipes, and glossa. Young (1977) and Young and Hermann (1980) studied the foraging habits of *P. clavata* and reported that *P. clavata* used its mandibles to feed on the plant species *Ochroma lagopus* by biting into a thin red line of tissue that ran along the ventral side of each petiole. After several minutes, the ant carried away a large droplet of clear liquid. *Paraponera clavata* also fed on *Eupatorium* by using its mandibles to scrape a yellowish tissue from the edges of older leaves where they join the petioles. Biting and scraping tissue to obtain liquid is probably aided by the adaptive sharp point located at the area where distal and ventral sides of the mandible join. The curvature and cradling effects of the mandibles, the setae which line the ventral and dorsal sides of the mandible, and the increased overall length and width of the mandible, help to form, suspend, and protect the droplet of liquid when being harvested and transported. It is also clear that the mandibles work in concert with the labrum and stipetes to suspend liquid food sources.

The labrum and stipes form a flattened surface ventrally. The labrum is a flat, plate-like organ which can move proximal or distal with respect to the hypostoma; the stipes move laterally or medially with respect to the mid-line. The labrum and stipes, when extended fully, greatly increase the breadth of the maxillo-labial structure. McCluskey and Brown (1972) noted that *P. clavata* can agitate a droplet of sucrose for 40 min without significant reduction of the size of the droplet. Such



Figures 5–8. Mouthparts of *Paraponera clavata* with stipes (s), hypostomal bridge (hb), labial palpi (lp), maxillary palpi (mp), galea (ga), premental shield (ps), glossa (g), clypeus (c), labrum (l), and lacinial gonia (lg) labeled. 5. Maxillo-labial apparatus, glossa retracted, right lateral view (bar = 4.5×10^{-4} m). 6. Maxillo-labial apparatus, glossa retracted, ventral view (bar = 4.5×10^{-4} m). 7. Maxillo-labial apparatus, glossa retracted, dorsal view (bar = 5×10^{-4} m). 8. Maxillo-labial apparatus, glossa extended, dorsal view (bar = 3.3×10^{-4} m).



Figures 9–12. Mouthparts of *Paraponera clavata* with glossa (g), mandibles (m), and galea (ga) labeled. 9. Maxillo-labial apparatus, glossa extended, ventral view (bar = 5×10^{-4} m). 10. Glossa and galeal crowns (bar = 1.3×10^{-4} m). 11. Glossa ultrastructure (bar = 4.2×10^{-6} m). 12. Subglossal brush (bar = 8.9×10^{-6} m).

agitation is most likely due to the labrum and stipetes moving in concert with the labial palpi.

The glossa (analogous to the tongue) is reported by Gotwald (1969) as a protrusible membranous structure covered with a series of transverse ridges. Gotwald commented on the difficulty he had in preparing the glossa for study and his drawings reflect that difficulty in the lack of morphological information about the glossa. The SEM photographs in this study clearly show the glossa of *P. clavata* to be much more intricate than previously supposed. The highly modified cup-like setae, previously thought to be simply membranous ridges, appear to contribute significantly to *P. clavata*'s ability to harvest and transport liquid food sources. The glossa's intricate and complex structure increases the total surface area available for liquid–surface interaction, and its numerous cupped setae are specifically advantageous for the gathering and retention of liquid food sources.

Acknowledgments

We thank Jennifer L. Schuyler, James V. Allen, Connie Swensen, and William M. Hess for advice in the preparation of this manuscript. The Department of Zoology, Brigham Young University, provided funding for this project. The Smithsonian Tropical Research Institute, Balboa, Republic of Panama, provided housing and logistic support.

Literature Cited

Bennett, B., and M. D. Breed. 1985. On the association between *Pentaclethra macroloba* (Minosaceae) and *Paraponera clavata* (Hymenoptera: Formicidae) colonies. Biotropica, 17:253–255.

Breed, M. D., and B. Bennett. 1985. Mass recruitment to nectar sources in *Paraponera clavata*: a field study. Insect. Soc., Paris, 32:198–208.

Bugnion, E. 1924. Le sac infrabuccal et le pharynx des fourmis. Soc. Biol. Compt. Rend., 91:998–1000.

———. 1925. Notes relatives a la terminologie des organes buccaux des insectes. Soc. Zool. France Bull., 50:352–358.

———. 1930. Les pieces buccales, le sac infrabuccal et le pharynx des fourmis. Soc. Roy. Entomol. Egypte Bul., 14:85–210.

Crampton, G. C. 1923. A phylogenetic comparison of the maxillae throughout the orders of insects. J. N.Y. Ent. So., 31:77–107.

———. 1928. The eulabium, mentum, submentum and gular region of insects. J. Entomol. Zool., 21:1–18.

Cromroy, H. L., F. W. Zettler, W. R. Carpenter, and M. S. Elliott. 1987. A new mite pest on wax myrtle in Florida (Acari: Eriophyidae). Fla. Entomol., 70(1):163–167.

Duporte, E. M. 1967. Morphology of the first and second maxillae of insects. Can. J. Zool., 45:1269–1273.

Eisner, T., and G. M. Happ. 1962. The infrabuccal pocket of a formicine ant: a social filtration device. Psyche, 69:107–116.

Erickson, E. H., Jr., S. D. Carlson, and M. B. Garment. 1986. A scanning electron microscope atlas of the honey bee. The Iowa State Univ. Press, Ames, Iowa, 292 pp.

Gotwald, W. H., Jr. 1969. Comparative morphological studies of the ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). Mem. Cornell U. Agr. Ex. Sta., 408 pp.

Harrison, K. 1987. Deep-sea asellote isopods of the northeast Atlantic: the family Thambematidae. Zool. Scri., 16(1):51–72.

Hermann, H. R. 1975. Crepuscular and nocturnal activities of *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). Entomol. News, 86:94–98.

———, M. S. Blum, J. W. Wheeler, W. L. Overal, J. O. Schmidt, and J. T. Chao. 1984. Comparative anatomy and chemistry of the venom apparatus and mandibular glands in *Dinoponera grandis* (Guerin) and *Paraponera clavata* (F.) (Hymenoptera: Formicidae: Ponerinae). Ann. Entomol. Soc. Am., 77:272–279.

Huxley, T. H. 1878. A manual of the anatomy of invertebrate animals. D. Appleton and Company, New York, 596 pp.

Janet, C. 1899. Essai sur la constitution morphologique de la tete de l'insect. George Carre et C. Naud, Editeurs, Paris, 74 pp.

———. 1904. Observations sur les fourmis. Limoges, Imprimerie-librairie Ducourtieux et Gout., Paris, 68 pp.

———. 1905. Anatomie de la tete du *Lsius niger*. Limoges, Imprimerie-librairie Ducourtieux et Gout., Paris, 40 pp.

Janzen, D. H., and C. R. Carroll. 1983. *Paraponera clavata* (Bala, giant tropical ant). Pp. 752–753 *in* D. H. Janzen (ed.), Costa Rican natural history. University of Chicago Press, Chicago and London.

Liu, C. L. 1925. Observations on the acroglossal buttons and on the submentum of Hymenoptera. Ann. Entomol. Soc. Am., 18:445–455.

Marcus, H. 1944. Estudios mirmecologicos. I. Estudio comparado de la articulacion mandibular en las hormigas y termites. Acta Zool. Lilloana, 2:259–284.

Matsuda, R. 1965. Morphology and evolution of the insect head. Amer. Entomol. Inst., Ann Arbor, Michigan, 334 pp.

McCluskey, E. S., and W. L. Brown, Jr. 1972. Rhythms and other biology of the giant tropical ant *Paraponera*. Psyche, 79:335–347.

Michener, C. D., and R. W. Brooks. 1984. A comparative study of the glossae of bees (Apoidea). Contrib. Am. Entomol. Inst., 22(1):1–73.

Nelson, C. R., and R. W. Baumann. 1987. Scanning electron microscopy for the study of the winter stonefly genus *Capnia* (Plecoptera: Capniidae). Proc. Entomol. Soc. Wash., 89(1):51–56.

Peng, Y. S., and J. M. Marston. 1986. Filtering mechanism of the honey bee proventriculus. Physiol. Entomol., 11:433–439.

Snodgrass, R. E. 1956. Anatomy of the honey bee. Comstock Publishing Associates, Ithaca and London, 334 pp.

Steinmann, H., and L. Zombori. 1981. An atlas of insect morphology. Akad. Kiado, Budapest, Hungary, 248 pp.

Szlzytko, S. W., and R. L. Bottorf. 1987. *Consomnoperla hypocrena,* a new genus and species of western *Neartic isoperlinae* (Plecoptera: Perlodidae). Pan-Pac. Entomol., 63(1):65–74.

Young, A. M. 1977. Notes on the foraging of the giant tropical ant *Paraponera clavata* (Formicidae: Ponerinae) on two plants in tropical wet forest. J. Ga. Entomol. Soc., 12:41–50.

———, and H. R. Hermann. 1980. Notes on foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). J. Ks. Entomol. Soc., 53:35–55.

Publication Received

A Revision of the Neotropical Species of *Parabezzia* (Diptera: Ceratopogonidae). By Gustavo R. Spinelli and William L. Grogan, Jr. Biologia Acuatica, no. 11:1–45, figs. 1–15. Received by PCES at CAS on 12 November 1987. Published by the Instituto de Limnología "Dr. Raul A. Ringuelet," La Plata, Argentina. Price: US $4.00 (including postage). Available from Hugo L. López, Instituto de Limnología, Casilla de Correo 55, 1923 Berisso, Argentina. (It is requested that checks and money orders should be written to the name of Hugo L. López.) ISSN 0326-1638.

This photo reproduced article revises 23 Neotropical species of *Parabezzia,* of which 14 species are fully described and illustrated, and a diagnosis is provided for each of nine other species. A key to species (primarily to females) appears on pages 7–10. Included are nine new species: *Parabezzia balseiroi* (pp. 13–17; Argentina), *P. clastrieri* (pp. 23–25; El Salvador, Belize), *P. hondurensis* (pp. 25–27; Honduras), *P. pseudunguis* (pp. 30–32; Panama), *P. brasiliensis* (pp. 34–36; Brasil), *P. cayoensis* (pp. 36–38; Belize), *P. inaequalis* (pp. 38–40; Brasil), *P. pallida* (pp. 40–41; Mexico), and *P. raccurti* (pp. 42–44; El Salvador).—Paul H. Arnaud, Jr., California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.